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SPECIES OF SPIDERS (ARANEAE) ASSOCIATED WITH THE IMMATURE STAGES OF *MANTISPA PULCHELLA* (NEUROPTERA, MANTISPIDAE)

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ABSTRACT

Species of spiders associated with the immature stages of *Mantispa pulchella* (Banks) are presented for the first time. Twenty species in 15 genera from the families Philodromidae, Anyphaenidae, Oxyopidae, Thomisidae, and Salticidae harbored immature stages of *M. pulchella* in South Carolina. Some characteristics of the life history of *M. pulchella* are analyzed and compared with those of other North American species of Mantispinae.

The cosmopolitan family Mantispidae was recently divided into the subfamilies Symphrasinae, Drepanicinae, Calomantispinae, and Mantispinae (Lambkin 1986). Little is known about the life histories of the first three subfamilies. Several species of the Symphrasinae have been associated with nests of aculeate Hymenoptera as well as with pupae of Noctuidae and Scarabaeidae (Parker and Stange 1965), and one species of the Drepanicinae has been associated with a spider egg sac (Austin 1985). Natural history of the Calomantispinae remains unknown, although MacLeod and Redborg (1982) suggested, based on laboratory rearings, that larvae of the Symphrasinae and Calomantispinae were generalist predators of sedentary arthropod prey. In contrast, adult Mantispinae have been reared exclusively from spider egg sacs (Redborg and MacLeod 1985; Brushwein 1986).

Female mantispines are not known to oviposit either on spider egg sacs or on spiders, and instead deposit clutches of approximately 200 to 2000 stalked eggs on leaves, pieces of wood, and other objects (McKeown and Mincham 1948; LaSalle 1986; Rice 1986b). Following eclosion, larvae locate and gain access to spider eggs by using one or both of two general strategies. Larvae may either seek out and penetrate previously deposited egg sacs or board female spiders and enter egg sacs as they are being formed (Redborg and MacLeod 1985). Larvae feed on

spider eggs by piercing the chorion and draining the contents. Pupation occurs within the egg sac, and pharate adults exit both their own cocoons and the egg sacs before emerging from the pupal skin.

The mantispine *Mantispa pulchella* (Banks) has been recorded previously from Utah, southern Illinois, Georgia, North Carolina, and Panama (Banks 1912; Hughes-Schrader 1969; Redborg 1976; Hoffman and Hamilton 1988). Both Redborg and MacLeod (1985) and Brushwein (1986) reported the successful rearing of this species during studies on other species, but no further details were presented. The present paper records the presence of *M. pulchella* in South Carolina for the first time, documents spider associations, analyzes some characteristics of the life history of this species, and compares these characteristics with those of other North American Mantispinae.

METHODS

The majority of the immature stages of *M. pulchella* and associated spiders were collected by the authors from March 1986 through April 1988 in and around Clemson, Pickens County, South Carolina. Spiders and spider egg sacs of as many different taxa as could be collected visually were examined for the presence of mantispine immatures. In addition, the spider collection within the Clemson University Arthropod Collection (CUAC) was searched and eight first instar *M. pulchella* were located. Prior to the present study, the CUAC contained 29 families, 101 genera, and 162 species of spiders from South Carolina (Gaddy and Morse 1985). However, the collections made during the course of the present study, that of Brushwein (1986), and the identification of previously undetermined material encountered during examination of the CUAC have increased the collection to 32 families, 167 genera, and 290 species.

Four adult *M. pulchella* were collected in 1986 in an ultraviolet light trap run nightly from January 1984 to October 1986, and 52 additional adults were located in the CUAC. The latter specimens had been collected from the South Carolina counties of Barnwell, Dorchester, Florence, Oconee, Pickens, and York from 1956 to 1986.

Identity of the immature stages of *M. pulchella* was confirmed by the subsequent rearing of some (n = 18) to adults, using procedures detailed elsewhere (Brushwein 1986). Some juvenile spiders were also reared to maturity for species-level identifications. Spiders were identified both by the use of selected taxonomic references (Edwards 1958; Kaston 1973; Platnick 1974; Dondale and Redner 1976, 1978; and Roth 1985) and with the kind assistance of A. R. Brady, G. B. Edwards, J. H. Redner, and S. H. Roach. Voucher specimens of *M. pulchella* and associated spiders were deposited in the CUAC, Department of Entomology, Clemson University.

RESULTS

Spiders were each associated with a single immature *M. pulchella*. First instars of *M. pulchella* were found either wrapped dorsally over the pedicel and posterior edge of the carapace of spiders (Fig. 1) or inside spider egg sacs, whereas all other immature stages were found only inside egg sacs. Spiders with larvae on them

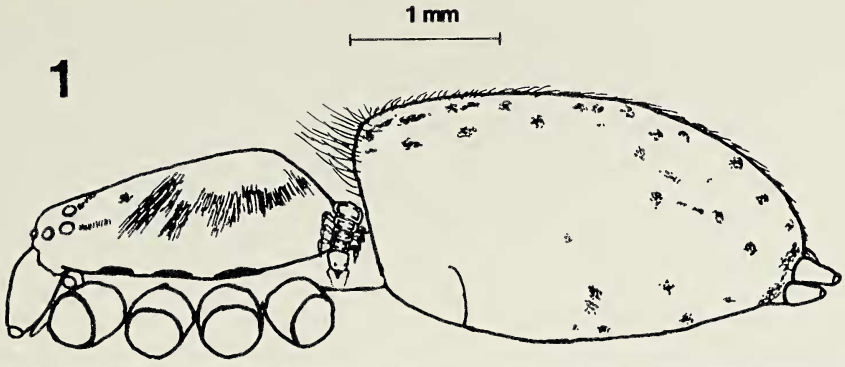

Figure 1.—Juvenile *Anyphaena* sp. with *Mantispa pulchella* larva in dorsal pedicel region, left lateral view. Palpal and leg segments distal to coxae omitted.

usually had discolored patches present on one or both sides of the pedicel; these patches were located ventrolaterally on the anterior portion of the pedicel or on the membranous area just below the posterior edge of the carapace. The dark patches were at the approximate location that larval mouthparts would come in contact with the spider integument.

Members of the family Anyphaenidae were the most commonly collected spiders associated with *M. pulchella* and comprised 65.7% (n = 134) of the records, followed by members of the Salticidae and Clubionidae at 19.4% and 10.4%, respectively (Table 1). The families Philodromidae, Oxyopidae, and Thomisidae combined for the remaining 4.5%. Larvae were associated with adults as well as with penultimate and earlier instars; and of the 87 spiders whose gender could be determined, 53 were males and 34 females. First instars of *M. pulchella* were found during all months, whereas all other immature stages were found only during May and June (Table 2). Adults were collected from May to September, with the majority collected during July.

DISCUSSION

The presence of *M. pulchella* larvae on spiders confirms that this species boards spiders to gain access to spider eggs. Five other North American species have been studied with respect to their strategies for gaining access to eggs. First instars of *Mantispa viridis* Walker located and entered previously deposited egg sacs and fed directly on the eggs within; larvae would not board spiders and therefore were termed obligate penetrators of egg sacs (Redborg and MacLeod 1985; Brushwein 1986). In contrast, first instars of *Climaciella brunnea* (Say) did not penetrate previously constructed egg sacs and would not feed on spider eggs unless larvae had previously been aboard spiders; larvae readily boarded spiders and were termed obligate spider boarders (Redborg and MacLeod 1983). Recent studies on neonate *M. pulchella* larvae have similarly failed to induce larvae to feed on spider eggs unless larvae had previously boarded spiders (Brushwein and Hoffman unpubl.). First instars of *Mantispa uhleri* Banks are facultative spider boarders because although they showed a strong preference for spider boarding over direct egg sac penetration, they could still penetrate egg sacs and develop without previously having boarded spiders (Redborg and MacLeod 1985). First

Table 1.—Spider taxa associated with immature stages of *Mantispa pulchella* in South Carolina. Numbers represent the number of collections of each taxon, broken down by developmental stage and gender. Superfamilies and families are arranged according to the taxonomic list presented by Shear (1986). (undet. = gender undetermined).

SUPERFAMILY Family Species	Developmental stage and gender					
	Adults		Juveniles			Egg sacs
	Male	Female	Male	Female	Undet.	
CLUBIONOIDEA						
Clubionidae						
Clubiona maritima L. Koch	0	1	0	0	0	0
Clubiona obesa Hentz	1	0	3	2	0	1
Clubiona sp., poss. *obesa*	0	0	1	0	2	0
Clubionoides excepta (L. Koch)	1	0	0	0	2	0
PHILODROMOIDEA						
Philodromidae						
Philodromus imbecillus Keyserling	0	0	0	0	0	1
Philodromus vulgaris (Hentz)	1	1	0	0	0	0
DICTYNOIDEA						
Anyphaenidae						
Anyphaena fraterna (Banks)	2	1	0	0	0	0
Anyphaena pectorosa L. Koch	0	1	1	1	0	0
Anyphaena sp., *pectorosa* group	0	0	21	7	23	0
Aysha gracilis (Hentz)	1	1	2	5	2	0
Teudis mordax (O. P.-Cambridge)	0	1	0	0	0	9
Wulfila albus (Hentz)	0	2	3	2	3	0
LYCOSOIDEA						
Oxyopidae						
Oxyopes aglossus Chamberlin	0	0	0	0	1	0
THOMISOIDEA						
Thomisidae						
Misumenops asperatus (Hentz)	0	0	1	1	0	0
SALTICOIDEA						
Salticidae						
Eris marginata (Walckenaer)	2	0	0	0	0	0
Hentzia palmarum (Hentz)	0	1	4	2	1	0
Lyssomanes viridis (Walckenaer)	0	0	0	0	1	0
Maevia inclemens (Walckenaer)	0	0	0	1	0	0
Metacyrba undata (De Geer)	1	0	0	0	0	0
Metaphidippus exiguus (Banks)	7	3	0	0	0	0
Metaphidippus galathea (Walckenaer)	1	0	0	0	0	0
Metaphidippus peckhamorum Kaston	0	0	0	0	0	1
Metaphidippus sp.	0	0	0	1	0	0
Totals	17	12	36	22	35	12

instars of *Mantispa fuscicornis* Banks have been found on six species of spiders (Rice 1986b). In light of the current status of this species as a sibling species of *M. uhleri* (Hughes-Schrader 1979), *M. fuscicornis* larvae are probably also facultative boarders. Larvae of *Mantispa interrupta* Say have boarded and remained on a spider in the laboratory (Viets 1941), and recent studies indicate that larvae of this species are facultative spider boarders (Brushwein unpubl.). The behavior of *M. pulchella* larvae seems to be more similar to that of *C. brunnea* larvae than to that of other North American mantispine larvae, and therefore *M. pulchella* larvae are probably obligate boarders as well.

Table 2.—Number of *Mantispa pulchella* collected by month in South Carolina.

	M. pulchella Developmental stage				
Month	First	Second	Third	Pupa	Adult
January	17	0	0	0	0
February	4	0	0	0	0
March	6	0	0	0	0
April	15	0	0	0	0
May	6	1	0	0	3
June	2	3	1	6	2
July	1	0	0	0	46
August	12	0	0	0	3
September	13	0	0	0	2
October	12	0	0	0	0
November	15	0	0	0	0
December	20	0	0	0	0
Totals	123	4	1	6	56

Both the position occupied while on spiders and the number of larvae on each spider appear different for *M. pulchella* than for other species. *Mantispa pulchella* larvae were found wrapped over the dorsal pedicel region and only one larva was found per spider. In contrast, first instars of *M. uhleri* have been found wrapped either dorsally, ventrally, or laterally around the pedicel, inside the book lung slits, or, less commonly, on the membrane between the carapace and leg bases, on the legs, or around the spinnerets; some spiders had two or three larvae on them (Redborg and MacLeod 1985). Larvae of *M. fuscicornis* have been found wrapped ventrally around the pedicel, inside the book lung slits, or, less commonly, on the membrane between the carapace and leg bases or on a leg (Rice 1986b); it was not uncommon to find 2 or 3 larvae per spider (M. Rice pers. comm.). *Climaciella brunnea* larvae have only been found associated with the carapace and the membrane between the carapace and the leg bases; the presence of two larvae on a spider has been reported (Redborg and MacLeod 1983). The variability in the positions occupied by larvae of these other species affords multiple resting sites on a single spider and the large size of some of the hosts (e.g., the Lycosidae) allows for more than one larva in areas such as the pedicel region or carapace. In contrast, the combination of a single resting site and the relatively small size of the spiders associated with *M. pulchella* would seem to preclude multiple infestations.

First instar *M. pulchella* may sustain themselves by feeding on the hemolymph of the boarded spiders, thereby becoming true ectoparasites. Abdomens of larvae commonly were distended to the point that the abdominal banding pattern became diffuse. Similarly, first instars of *M. uhleri* on spiders appeared "plumper" than neonate larvae and were found to gain weight after boarding spiders (Redborg and MacLeod 1984). Also, the discolored patches on spiders boarded by *M. pulchella* appeared to be similar to those on spiders boarded by *M. uhleri*, which Redborg and MacLeod (1984) interpreted as evidence of larval feeding damage. If this interpretation is correct, then the occurrence of patches on both sides of a single pedicel indicates that *M. pulchella* larvae either occasionally reverse their orientation while on spiders or that the spider had been infested prior to the boarding by the current occupant.

The behavioral and morphological parameters of spiders that permit successful mantispine boardings are virtually unknown. However, the spiders associated with *M. pulchella* do share a few ecological and behavioral characteristics. All spiders were wanderers which do not build webs for prey capture and which are commonly found on foliage (Kaston 1978). In addition, members of the Anyphaenidae, Salticidae, and Clubionidae all construct tubular silken retreats for resting and molting in harborages such as curled leaves and beneath bark. Members of the Philodromidae, Oxyopidae, and Thomisidae do not. Therefore, while *M. pulchella* larvae appear to board primarily wandering spiders on foliage, spiders within retreats might be easier for larvae to locate or board than those not in retreats.

Five other North American mantispine species have been associated with spiders. Redborg and MacLeod (1985) found that *M. uhleri* larvae were associated with a wide variety of wandering spiders and attributed the lack of associations with web-building spiders to the inability of larvae to come into contact with spiders suspended in webs. Similarly, all spiders associated with *C. brunnea* larvae also were wanderers, namely the ground cursorial Lycosidae (LaSalle 1986; Redborg pers. comm.). *Mantispa fuscicornis* larvae were associated with both web-building and wandering spiders, but Rice (1986b) hypothesized that the presence of larvae on web-builders was due to the tendency of those particular species to retreat into the cracks and corners of a wooden shelter during the day and therefore became more accessible to larvae searching on that substrate. Larvae of *M. interrupta* have only been associated with three species of wandering spiders (Redborg and MacLeod 1985; Rice 1986a). In contrast, *M. viridis* larvae have been associated with a wide variety of both web-building and wandering spiders (Brushwein 1986). The above findings on other species coupled with the present data on *M. pulchella* suggest that mantispine species that use spider boarding to gain access to spider eggs generally will be associated with wandering spiders, whereas species whose larvae normally locate and penetrate previously deposited egg sacs will be associated with a wider diversity of both web-builders and wanderers.

The male to female ratio of 53 to 34 for spiders associated with *M. pulchella* seems in contrast to what might be expected, given that larvae board spiders in order to gain access to eggs. However, if the twelve infested egg sacs can be taken as an indication of larvae having boarded females prior to their oviposition, then the male to female ratio becomes essentially one to one (53 to 46). In any case, the male to female ratio of *M. pulchella* correlated well with results obtained by Redborg and MacLeod (1985) on *M. uhleri*, where the male to female ratio of spiders was 48 to 36 and where larvae boarded spiders of both genders with equal frequency in the laboratory.

The subsequent fate of *M. uhleri* larvae on male spiders was unclear because larvae failed to transfer from males to females when mating occurred. However, some larvae transfered from conspecific males to females when the male was cannibalized. Redborg and MacLeod (1985) argued that transfer of larvae during mating would require larvae to coordinate their transfer activities with the wide variety of courtship behaviors exhibited by the various spider species. In contrast, transfer of larvae during cannibalism required no such coordination and had the advantage of larval transfer from any spider to any other, regardless of sex, developmental stage, or species. The ability of larvae to transfer from one spider

species to another in this manner could therefore result in occasional transfers of larvae to spider species which for behavioral or morphological reasons would not normally be boarded by larvae of that particular mantispine species. Therefore, spider associations for a particular mantispine species could consist both of spider species which are normally boarded and of species which are not normally boarded but which acquired larvae via predation of infested spiders. Unfortunately, the extent to which the spider associations of *M. pulchella* reflect the latter category cannot be assessed at this time.

The presence of first instars of *M. pulchella* on spiders throughout the winter indicates that this species overwinters on spiders. Furthermore, the absence of any other developmental stages of *M. pulchella* during the winter months suggests that *M. pulchella* overwinters in South Carolina only as first instars on spiders. This species also may overwinter as eggs, but the lack of egg collections coupled with reports on the larval or pupal overwintering strategies of other species argues against this. Redborg and MacLeod (1985) concluded that *M. uhleri* overwintered in southern Illinois exclusively as first instars on spiders, and Brushwein (1986) concluded that *M. viridis* overwintered in northwestern South Carolina as either larvae or pupae within spider egg sacs.

The collection of second instar *M. pulchella* during May and June, of third instars and pupae during June, and of most adults during July indicates that this species is essentially univoltine in South Carolina. However, the possibility for more than one generation per year cannot be excluded. Additional generations could result from adult *M. pulchella* produced by spiders which bred early in the year subsequently producing larvae that board spider species destined to breed later in the year. Redborg and MacLeod (1985) and Brushwein (1986) discussed similar scenarios in relation to the seasonal cycles of *M. uhleri* and *M. viridis*, respectively. The spiders associated with both *M. uhleri* and *M. viridis* included species which bred during late summer and fall and, accordingly, an average of two generations per year was reported for *M. uhleri* in Illinois and a minimum of three generations were observed for *M. viridis* in South Carolina. However, no immature *M. pulchella* were found either on adult spiders or inside egg sacs from August until late December, indicating that the spider species used by *M. pulchella* all breed earlier in the year.

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